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AMERICAN AMPHICŒLIAN CROCODILES

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As long ago as 1849, Sir Richard Owen described[1] a genus (*Hyposaurus*) of amphicœlian crocodiles from the Cretaceous of New Jersey, based upon imperfect anterior dorsal vertebræ, whose chief characteristic was the unusual development of the hypapophyses. But little has been added to our positive knowledge of the genus since its original description, though the remains of such animals are said to be common in the New Jersey deposits. Leidy, in 1865, described and figured[2] other vertebræ, and also assigned to the same genus certain fragments of hollow propodial bones. Cope, in 1869, also described[3] additional vertebræ and limb bones, with illustrations, but I think there is much uncertainty as to the correlation of these limb bones with the vertebræ. He also mentioned certain parts of the skull, from which it would appear that Owen was correct in locating his genus among the longirostres. However, Cope at the same time referred portions of the rostrum of one specimen from the same horizon and same locality as those of the specimens which he referred to *Hyposaurus rogersi* Owen, to a distinct species, under the name *Hyposaurus fraterculus*, but which he afterward removed[4] to the genus

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[1] Owen, *Quarterly Journal of the Geological Society*, Vol. V (1849), p. 383.

[2] Leidy, *Cretaceous Reptiles*, p. 18, Plate III, Figs. 4, 16–21; Plate IV, Figs. 1–12.

[3] Cope, *Extinct Batrachia*, etc. (1869), p. 80, Plate IV, Figs. 10, 11.

[4] Cope, *Cretaceous Vertebrata* (1875), p. 254; *Proceedings of the Academy of Natural Sciences*, Philadelphia, 1875, p. 19.

Gavialis, where it remains to the present time, though doubtless belonging in one or another of the tomistomid genera which have been described from the New Jersey deposits, if not really a *Hyposaurus*, as Cope first believed.

Leidy founded the genus and species *Thoracosaurus grandis* upon dermal plates from the same horizon.[1] He later assigned to the same species,[2] under the name *Thoracosaurus neocesariensis* De Kay,[3] an excellent skull, unassociated with other bones. I have read attentively Leidy's descriptions and remarks, as also those of Cope, concerning this and other specimens referable to this species, and nowhere do I find a positive collocation of the type with procœlous vertebræ, though Leidy assigned to the species the procœlous vertebræ previously described by Owen as *Crocodilus basifissus*.[4] It is probable, however, that *Thoracosaurus* is really a procœlian crocodile, since *Holops* Cope, a nearly allied, if not identical, genus, has been definitely associated with procœlous vertebræ.[5] Furthermore, Koken referred to the same genus,[6] though with some hesitancy, a skull from the Maastrichtian of northern Germany, which he identified specifically with *Thoracosaurus macrorhynchus* (Blaineville) Leidy,[7] originally described from the Lower Eocene of Germany. This geographical distribution is not at all remarkable, since we know that the genus *Mosasaurus* has a like distribution in the Maastrichtian of Belgium and the Cretaceous of New Jersey, as also the Pierre of the interior. We may, therefore, accept both *Thoracosaurus* and *Holops* as procœlian crocodiles, though further information as to the skeletal structure of each is highly desirable.

As to the third genus of crocodiles reputed to be procœlian from the Cretaceous of New Jersey, *Bottosaurus* Agassiz,[8] I do not think matters are as satisfactory. It is evident that the type species of the genus, *B. harlani* Meyer, is a broad-faced or brevirostrate form, but I do not feel so sure that it has procœlous vertebræ. Harlan based his species *Crocodilus macrorhynchus* Harlan (non-Blaineville) upon the larger part of the right mandible, which has been figured and more fully described by Leidy.[1] This mandible is very peculiar in lacking, apparently, the large foramen, so characteristic of all procœlian crocodiles, ancient and modern, and of the known amphicœlian forms, save certain species of *Goniopholis*[2] and other Goniopholididæ, such as *Pterosuchus*.[3] Indeed, the Parasuchia or Phytosauria, which I would exclude from the Crocodilia in the widest sense, have such a foramen. Cope later added another species, *B. tuberculatus*,[4] to the genus, but I fail to find any positive evidence of congenerousness with the type species, nor am I assured that the form is brachystomous even. *B. perrugosus* Cope, which may be the same as *Crocodilus humilis* Leidy, from the Laramie Cretaceous of eastern Colorado, was only provisionally referred to the genus.[5] A gigantic procœlian crocodile is not at all uncommon in the uppermost Cretaceous of the West, as mentioned by Hatcher and as I have seen from western Texas. No other evidence is forthcoming that *Bottosaurus* has procœlous vertebræ. If it really has, then an important fact has been for the most part overlooked hitherto, the presence of broad-faced crocodiles, with a short mandibular symphysis, from so low an horizon, forms which might stand in more immediate ancestral relationship with the modern Crocodilidæ than do any of the known Tomistomidæ (Rhynchosuchidæ) of the Cretaceous. I cannot resist the suspicion that *Bottosaurus* will eventually be found to be an amphicœlian form. It is a remarkable fact, as Koken has shown,[6] that the early longirostrate procœlian crocodiles are scarcely distinguishable generically, save in their vertebræ, from their contemporary longirostrate amphicœlian forms, and it is altogether likely that a similar likeness existed in those early crocodilian times between the amphicœlian Bernissartidæ and such forms as *Bottosaurus* must have been if really procœlian. Marsh has stated, however, that there are several forms of amphicœlian crocodiles in the New Jersey deposits,[1] and has, indeed, named one of them *Hyposaurus ferox.*[2]

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[1] Leidy, *Proceedings of the Academy of Natural Sciences*, Philadelphia, Vol. VI (1852), p. 35.

[2] Leidy, *Cretaceous Reptiles* (1865), p. 5, Plates I–III.

[3] DeKay, *Zoology of New York*, Part III, p. 28, Plate XXII, Fig. 9 (*Gavialis*).

[4] Owen, *Quarterly Journal of the Geological Society*, Vol. V (1849), p. 381, Plate X, Figs. 1, 2.

[5] Cope, *Extinct Batrachia*, etc. (1865), p. 69, Plate I, Fig. 13.

[6] Koken, *Zeitschrift der Deutschen geologischen Gesellschaft*, 1888, p. 754.

[7] Leidy, *Cretaceous Reptiles* (1865), p. 8.

[8] Agassiz, *Proceedings of the Academy of Natural Sciences*, Philadelphia, Vol. IV (1849), p. 169.

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[1] Leidy, *Cretaceous Reptiles* (1865), p. 2, Plate IV, Figs. 19–23.

[2] Owen, *British Fossil Reptiles*, Vol. I, p. 642, Plate XLII, Fig. 2.

[3] Owen, *Fossil Reptiles of the Wealden Formation* (1878), Supplement VIII, p. 10.

[4] Cope, *Extinct Batrachia*, etc. (1865), p. 230.

[5] Cope, *Cretaceous Vertebrata* (1875), p. 68, Plate VI, Figs. 5–8.

[6] Koken, *Paleontologische Abhandlungen* (1887), Vol. III, p. 93.

Whatever may be the real truth in the case, that the upper New Jersey Cretaceous rocks have yielded the remains of longirostrate amphicœlian crocodiles seems definitely determined from certain remarks made long ago by Professor Cope incidentally in his description of *Hyposaurus derbianus* from Brazil.[3] These remarks have been so completely overlooked by all other writers upon fossil crocodiles, whether in textbooks or in technical papers, that I venture to quote them in entirety. Even Hay omitted reference to the paper in his remarkably complete catalogue of North American fossil vertebrates.

> The genus *Hyposaurus* has been hitherto represented by but one well-known species, the *H. rodgersi* Owen, of the Greensand of the Cretaceous No. 5[4] of New Jersey. Specimens in my possession demonstrate that the genus *Hyposaurus* belongs to the Teleosauridæ of St. Hilaire. It differs from *Metriorhynchus* Meyer in the presence of distinct lachrymal bones, and in the relatively small size of the prefrontals. From *Teleosaurus* proper it differs in the robust size and vertical direction of the teeth. The orbits are vertical and the sagittal region is a keel. In the *H. rodgersi* the frontal bone is narrower than in any of the species figured or described by Deslongchamps. The palatal foramina extend forward to the line of the posterior maxillary teeth, and the anterior border is rounded, not acute as in most species of the family. The specimens are not sufficiently complete to enable me to state positively the generic distinction from *Steneosaurus*. In *Teleosaurus* the vertebral hypapophyses only appear on the first and second dorsal vertebræ, while, as Owen observes, they are present on many of the dorsals in *Hyposaurus*. This peculiarity, and the great contraction of the frontal bone, render it very probable that the genus is distinct from *Steneosaurus*, but the diagnostic character yet remains to be discovered.

If the genus is closely allied to the true species of *Steneosaurus*, then it is quite certain that *Hyposaurus* is a member of the Teleosauridæ in the narrow acceptation. But Cope mentions no species, and it is now known that certain species referred to *Steneosaurus*, especially *S. geoffroyi* Owen,[1] do not belong in this genus,[2] or family even, but rather with the Pholidosauridæ, possibly *Pholidosaurus*. The lateral orbits which Cope gives for *Hyposaurus* is not a teleosaurid character. *S. geoffroyi* has elongated nasals, quite different from those of *Teleosaurus* proper, and it is probable that *Hyposaurus* will be found to possess them also, as in *Teleorhinus* Osborn. It is interesting to observe, however, that *Hyposaurus derbianus* "sends upward [from the jugals] a postorbital branch, which is external as in other Teleosauridæ, and not internal as in the Crocodilidæ"—a strong teleosaurid character that would remove the species from the Pholidosauridæ.

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[1] Marsh, *American Journal of Science*, Vol. XIV (1877), Sep. p. 14.

[2] Marsh, *Proceedings of the Academy of Natural Sciences*, Philadelphia, 1871. p. 104.

[3] Cope, *Proceedings of the Academy of Natural Sciences*, Philadelphia, Vol. XXIII; *Paleontological Bulletin*, No. 40 (1885).

[4] Doubtless the Manasquan Marls.

The horizon of *H. derbianus* is given by Cope as the equivalent of the "Fox Hills," that is of the Fort Pierre,[3] and perhaps equivalent to the New Jersey deposits. The specimen was from the province of Pernambuco.

A second genus of longirostrate amphicœlian crocodiles, from an earlier horizon, has been recently described by Osborn[4] from the Benton Cretaceous of Montana. Osborn separates the genus from *Hyposaurus* by the lesser curvature of the propodial bones, but, as I have stated, it is somewhat doubtful whether we actually know the propodials of *Hyposaurus* sufficiently well to afford this information, if at all; and the author seemed unaware that the longirostrate, if not teleosaurid, character of *Hyposaurus* is established. (The bones figured by Leidy do not show the curvature.) He compares the genus with *Teleosaurus*, to which there seems to be little real relationship, but does not compare it with such forms as "*Steneosaurus*" *geoffroyi*, which has elongated nasals, or with *Pholidosaurus* (*Macrorhynchus*), to which it does appear to be allied. *Teleosaurus* has short nasals and upwardly directed orbits, bordered posteriorly by a rather stout, external rim of bone; *Pholidosaurus* has lateral orbits, as described by Cope for *Hyposaurus* and Osborn for *Teleorhinus*, and nasals extending to the premaxillaries or anterior nares as in *Teleorhinus*. The elongation of the nasals occurs also in other longirostres, like *Teleidosaurus*, etc., as well as in most of the brevirostrate amphicœlian forms, such as *Goniopholis*, *Nanosuchus*, *Notosuchus*, and *Petrosuchus*. In all, or nearly all, reptiles having a greatly elongated mandibular symphysis, the splenial takes part in the union, as in *Teleidosaurus*, *Hyposaurus*, and other longirostrate amphicœlians, the gavials, plesiosaurs, *Champsosaurus*, etc. Most of the other characters given by Osborn for *Teleorhinus* are of wider than generic application, save the antero-posterior compression of the teeth, which also occurs in other of the long-snouted amphicœlian forms. It is therefore difficult to interpret the affinities of his genus prior to a more complete description of the excellent material upon which it was based. I have scarcely a doubt, however, that it belongs with the Pholidosauridæ rather than the Teleosauridæ.

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[1] Owen, *British Fossil Reptiles*, Vol. III, p. 144, Plate XVIII.

[2] Koken, *Paleontologische Abhandlungen* (1887), Vol. III, p. 91.

[3] Stanton and Hatcher, *Bulletin 257* (1905), United States Geological Survey, p. 66.

[4] Osborn, *Bulletin of the American Museum of Natural History*, Vol. XX (1904), p. 239.

During the past season several specimens, more or less fragmentary, of longirostrate crocodiles, including the posterior part of two skulls, quite different from each other, and cervical vertebræ were obtained from the Hailey shales of western Wyoming, by the University of Chicago party. I was first inclined to locate their horizon in the Niobrara, because of the presence of a distinctly Niobraran genus of plesiosaurs, but a more careful study of the stratigraphy of the Benton convinces me that it belongs somewhere in the Carlyle formation. The skulls both agree in having very narrow parietals, very large supratemporal fenestræ, small laterotemporal vacuities, and large orbits. The upward process from the jugal seems, in one of the specimens at least, to be internal, as in the Pholidosauridæ. I cannot distinguish either of the species at present from *Hyposaurus*, though it is not impossible that one or the other may be *Teleorhinus browni* Osborn. From the lowermost part of the Benton, just above the Dakota, Mr. William Reed some years ago collected a longirostrate skull in Wyoming. It would seem, hence, that crocodile remains are widely distributed throughout the Benton of the Rocky Mountain region.

In 1872 Cope named,[1] and in a later work figured,[2] a single vertebra from the supposed Benton Cretaceous of Kansas, which he referred to *Hyposaurus* under the specific name *H. vebbii* or *H. vebbianus*. The locality whence his type was obtained is such that its horizon can only be the upper part of the Lower Cretaceous. Cope believed at first that the form was longirostrate, and so indeed it may yet prove to be. Within recent years I have recognized various fragments of the skull and vertebræ of what are evidently brevirostrate crocodiles from what probably is the same horizon as that of the type of *H. vebbii*, in southern Kansas. Whether or not the form or forms which they represent are conspecific with *H. vebbii* remains to be proven, but there is no doubt of the occurrence of a brachystomous crocodile in the Comanche of Kansas.[1]

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[1] Cope, *Proceedings of the American Philosophical Society*, Vol. XII, p. 310.

[2] Cope, *Cretaceous Vertebrata* (1875), p. 52, Plate IX, Figs. 8, 8*d*.

In 1878 Professor Cope described[2] from the Morrison beds of southern Colorado the vertebræ of a small amphicœlian crocodile under the name *Amphicotylus lucasii*. In 1888[3] he collocated with these vertebræ a skull and various other bones, from the examination of which he reached the conclusion that the genus is identical with *Goniopholis* Owen, confined, so far as known otherwise, to the Purbeck and Wealden of England, Belgium, and northern Germany. In September of 1877, a few months prior to the appearance of Cope's description of *A. lucasii*, Professor Marsh briefly described[4] a genus and species of brachystomous amphicœlian crocodiles from the Morrison beds of Morrison, Colo., under the name *Diplosaurus felix*. I doubt not that the genus is identical with *Amphicotylus*, and, in much probability, the species is also identical with that of Cope. Marsh, however, refused to accept the synonymy of *Goniopholis*, figuring his species, without comment, in 1896[5] under its original name *Diplosaurus felix*. He, however, never gave any characters to distinguish his genus, and his figure shows, it is seen, a marked resemblance to those of various species previously assigned to *Goniopholis*, and especially *G. simus* Owen.[6] I have very recently examined the type specimen, and am more firmly convinced of its congenerousness with *Goniopholis.* We may, therefore, assume that both *Amphicotylus* and *Diplosaurus* are synonyms of *Goniopholis*, as did Zittel.[1]

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[1] Williston, *University of Kansas Geological Survey*, Vol. IV (1898), p. 78; Vol. II (1878), p. 391.

[2] Cope, *Bulletin of the United States Geological Survey of the Territories*, Hayden.

[3] Cope, *American Naturalist*, Vol. XXII (1888), p. 1106.

[4] Marsh, *American Journal of Science*, Vol. XIV (1877), p. 254.

[5] Marsh, *ibid.*, Vol. II (1896), p. 61.

[6] Owen, *Fossil Reptiles of the Wealden and Purbeck Formations* (1878), Supplement VIII, Plate V.

Marsh has also referred to the genus *Diplosaurus* a fragment of a propodial bone discovered by him in 1868 in the Baptanodon beds of the Uinta Mountains.[2] Inasmuch as it must be almost, if not quite, impossible to determine with any degree of assurance the generic affinities of his species from such very incomplete material as he possessed, and as his specimen has never been described or figured in the slightest, the name *D. nanus* Marsh must be considered as purely *nomen nudum.* The specimen may be of a brevirostrate crocodile, but, considering the beds in which it was found, it is far more probable that it really belongs with a dolichostomous form.

Very recently Dr. W. J. Holland has described and figured[3] an excellent skull from the upper Morrison beds of Freeze Out Mountains, Wyoming, as *Goniopholis? gilmorei.* While the author was justified in assigning a new specific name to his specimen, he has given us no distinctive characters, nor was it possible for him to do so. The pitting of the superior surface of the skull is quite unknown in either *G. lucasi* or *G. felix.* The former species was, as we have seen, based exclusively upon vertebræ, and no description or figure has ever been given of any part of a skull presumably or definitely conspecific with the type. The type specimen of *G. felix* does not exhibit the superficial markings, though doubtless it will when fully extricated from its matrix, to which is yet adherent the thin exterior portion from which the major part of the skull has been removed.

Such pitting of the superior surface of the skull is quite characteristic of the genus *Goniopholis* and allied forms, and while it is possible that a close comparison of uninjured specimens might reveal specific characters, such is doubtful. The low parapet of bone bordering the posterior inner margin of the superior temporal vacuity on the parietal and "mastoid" bones is of doubtful specific value, as one, I think, will be assured from the comparison of different skulls of modern crocodiles.

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[1] Zittel, *Handbuch der Paleontologie* (1890), Vol. III, p. 676.

[2] Marsh, *American Journal of Science*, Vol. XIV (1877), p. 346.

[3] Holland, *Annals of the Carnegie Museum*, Vol. III (1905), p. 431.

The teeth, as figured by Dr. Holland, are not unlike those of *Goniopholis tenuidens* Owen.[1] That the specimen belongs in the genus *Goniopholis* I have little or no doubt—at least there appears to be less difference between our species and certain European ones, than between the known European species. No procœlous vertebræ have ever been found in the Morrison beds, nor indeed any from below the Upper Cretaceous in any part of the world, unless the vertebræ figured some years ago by Seeley from the English Wealden are truly crocodilian in nature.[2] I cannot agree with Dr. Holland in the belief that the arrangement of the bones on the under side of the cranium of his specimen is like that of the modern crocodiles. The under part is somewhat injured posteriorly, as stated by Dr. Holland, and as I can corroborate from an examination of this specimen, the whole of the false palate back of the maxillæ wanting. We have no reason to assume, however, that the structure here differs materially from that of the Goniopholididæ in the boundaries of the posterior nareal openings; if it does agree with the modern crocodiles in this respect, it would of course remove the form from the Goniopholididæ and substantiate another generic appellation.

Of the four specific names that have heretofore been given to the goniopholidids from America, the three based upon specimens from the Morrison beds may all be valid, and it is not at all improbable that they represent more than one species; but, so far, we have no conclusive evidence that such is the case.

I may add that crocodilian teeth are widely distributed in the upper Morrison horizons, as also in the Comanche deposits of western Kansas.

Coelosuchus reedii, genus and species new.

Recently I have received for examination, from the University of Wyoming, through its curator of paleontology, Mr. William Reed, the remains of a large amphicœlian crocodile, evidently of a brachystomous form. They were collected during the past season by Mr. Reed in the vicinity of Wilcox, Wyo., in a dark shale of the Graneros division of the Benton, and below the heavily laminated shales which must be ascribed to the Mowrie beds of Darton. I have recognized what I believe to be the same horizon, also fossiliferous, two hundred miles or more to the northwest in Wyoming, lying below the laminated shales yielding numerous fish scales and fish bones. The Hailey shales lie some four hundred feet higher than this horizon, above the Mowrie shales, and above thin layers of limestone which may represent the Greenhorn limestones of Darton. Mr. Reed has traced the Wilcox fossiliferous horizon for about thirty miles into Carbon County on Troublesome Creek, where it also yields vertebrate fossils.

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[1] Owen, *British Fossil Reptiles*, Vol. I, p. 642.

[2] Seeley, *Quarterly Journal of the Geological Society*, 1887, p. 212.

The fossils sent me are for the most part more or less fragmentary and water-worn. They include two or three species of plesiosaurs, one of which seems closely allied to *Trinacromerum anonymum* Williston, from the Benton of Kansas; various fragments of the carapace and plastron of a large, thick-shelled turtle; the spine of a shark, not unlike those of *Corax* from the Cretaceous of Kansas; small shark teeth; and a large premaxillary bone with a single long tooth, whose systematic position I have not yet determined.

I can distinguish but a single species, among the crocodilian remains preserved, though they differ greatly in size and may in reality be of different forms. Of course, none of the bones can be associated together as of one individual.

The ilium (Fig. 1) differs from that of a modern crocodile in the greater elongation of the posterior process, and in the relatively less width of the bone. An ischium (Fig. 5) of a smaller individual differs in the less expansion of the distal end, its more rounded posterior angle, and the greater obliquity of the shaft of the bone. The pubes of several individuals are represented by more or less fragmentary parts, all of about one size. One nearly complete specimen is shown in Fig. 2. It is also noticeable for the slenderness of the shaft, and the moderate dilatation of the distal extremity, differing markedly in this respect from the known forms of *Goniopholis* and *Bernissartia*. The upper extremity of a humerus of a large individual is shown in Fig. 3. Its curvature is slight, much less than of a humerus of nearly equal size of a longirostrate form from the Hailey shales. Other smaller humeri are present, nearly complete. They are slender and nearly straight, the lower extremity scarcely differing from that of a modern alligator or crocodile. The distal end of a tibia and its distal face are shown in Figs. 6 and 7. The proximal and distal ends of two large coracoids are shown in the figure. I have outlined the connecting part between them as would seem natural. The distal extremity is also noticeable for its moderate expansion.

The numerous vertebræ preserved are of various sizes and from various places in the vertebral column. A cervical (Fig. 8) has its extremities almost amphiplatyan; the hypapophysis is small; the parapophysial articulations are not large and are situated near the end. The neurapophyses are attached by a loose suture. The length of the vertebra is 50 mm; its width, 44 mm. A dorsal centrum, of which the anterior articular surface is shown in Fig. 9, has a very smooth surface exteriorly, and is but gently concave longitudinally. The posterior central articular surface is nearly flat, the anterior rather deeply cupped. The length of the centrum is 59 mm; its width, 50 mm. Another centrum (Fig. 10) is much more compressed from side to side, presenting a vertically oval figure at the ends and in cross-section. This centrum has a length of 50 mm and a width of but 36 mm. The largest (dorsal) centrum preserved has a length of 65 mm and width of 70mm.

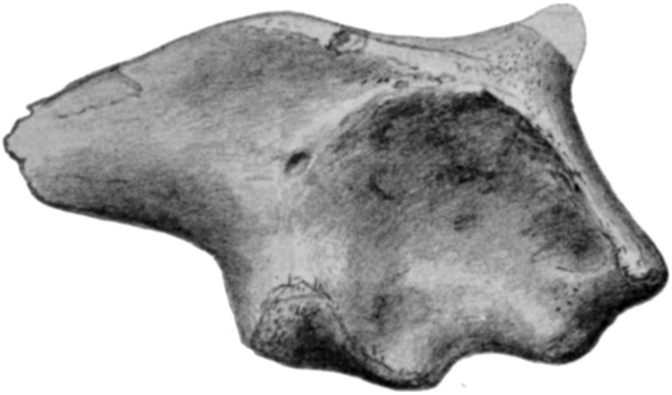

FIG. 1.—*Coelosuchus reedii.* Right ilium, one-half natural size.

Various fragments of the skull are preserved, but no teeth can be detected, though a fragment of a dentary or maxilla has numerous thecæ for their reception. The skull fragments are massive and deeply pitted, conclusively proving, it seems to me, the brachystomous nature of the face. The largest portion preserved is that figured herewith, the posterior part of the left mandible. It measures 155^{mm} in its greatest width, and resembles the corresponding part of the mandible of *Goniopholis tenuidens*, as figured by Owen.[1] If the skulls of the two species were of like proportions, the present must have measured over four feet in length. Species of *Goniopolis* have no mandibular foramen, so characteristic of the crocodiles, and its absence in the present species, together with the great width of the bone and its numerous deep pittings, indicates conclusively the brevirostrate character of the form. This is also indicated by the large size of the anterior extremities, the bones preserved showing that they were fully as large as the posterior ones, a character also seen in *Goniopholis* and *Bernissartia*, and very different from the small fore legs of the longirostrate types.

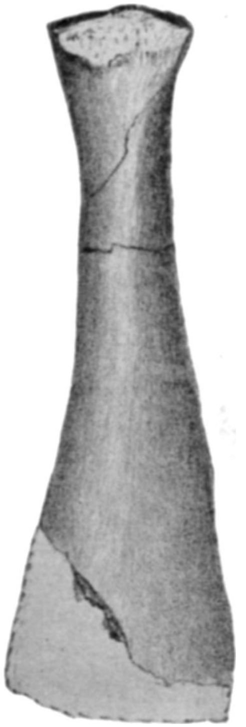

FIG. 2.—*Coelosuchus reedii.* Right pubis, one-half natural size.

The Goniopholididæ are supposed to have been denizens of fresh or brackish water, but these specimens do not necessarily imply that the Wilcox shales are of that character, since the bones may have been accumulated at the mouths of rivers or adjacent to the shores. However, some of the present Crocodilidæ are denizens of salt water, and it is not at all improbable that various extinct broad-faced species may have had similar habits. The turtle bones accompanying the remains are massive and heavy, very different from the typical marine types.

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[1] Owen, *British Fossil Reptiles*, Vol. II, Plate XLII, Fig. 2.

In conclusion, from the study of considerable material, and the attentive perusal and consideration of the facts and arguments offered, especially by Koken,[1] I share the opinion of most recent writers on the crocodilia that the separation of the amphicœlian and procœlian crocodiles by Huxley, which at one time seemed so brilliant a generalization, into the suborders Mesosuchia and Eusuchia is unnatural and artificial. I believe that the change from amphicœlous to procœlous vertebræ has been concurrent in two, possibly in all three, of the modern types of Crocodilia, the Gavialidæ, Tomistomidæ, and Crocodilidæ. In the specimens from the Hailey shales the centra may best be described as cœloplatyan, the anterior concavity deep, the posterior one shallow, if any. The change from this form to a distinctly procœlous one is not at all difficult to understand, and was brought about, I believe, by the same or similar causes in the different phyla. The true teleosaurs could not have been ancestral to any of the modern crocodiles, since the marked difference in the size of the fore and hind limbs was, a specialization for aquatic habits, as was carried to a greater degree in the Thalattosuchia,[2] and could not have reverted to the more modern amphibious type, even that of the gavials. That the true crocodiles began existence as terrestrial, or at least terrestro-amphib-

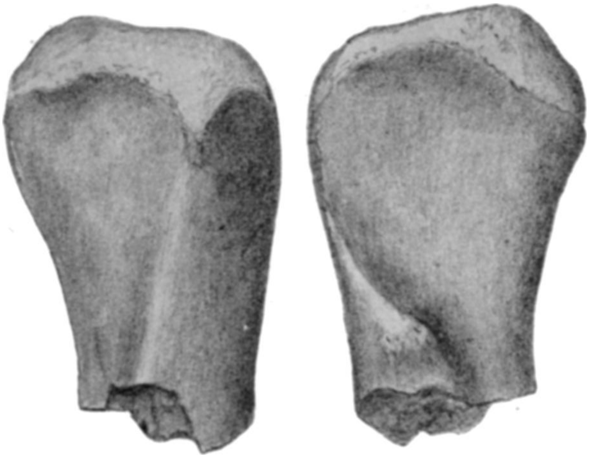

FIG. 3.—*Coelosuchus reedii.* Proximal extremity of right humerus, one-half natural size.

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[1] Koken, *Paleontologische Abhandlungen* (1887), Vol. III, p. 105; *Zeitschrift der Deutschen geologischen Gesellschaft*, 1888, p. 767.

[2] Fraas, *Paleontographica*, Vol. XLIX (1902), p. 1.

ious, animals is scarcely open to doubt, and all are agreed that the phytosaurs were not this ancestral type. That they should have become more aquatic in habit than are any now living, and again reverted to a subterrestrial habit, as in the modern alligators, is difficult, if not impossible, to believe. The true teleosaurs, like the thalattosaurs, were a short-lived branch of which no modern descendants have survived. Owen has thought[1] that the introduction and development of the small mammals was a cause of the evolution of the small, brevirostrate crocodiles, the Atoposauridæ and Goniopholididæ; but I doubt this very much, though they may have been the inciting cause of the evolution of such diminutive forms as *Alligatorellus* and *Atoposaurus*. Were more extensive land faunæ to be discovered in the middle and lower Jura, I believe that we should find the remains of real amphibious brachystomous crocodiles, much less like the structure of *Teleosaurus* than is *Teleidosaurus* even. It is hard to believe that the littoral reptiles, or semiaquatic forms, like *Pleurosaurus*, *Acrosaurus*, etc.,

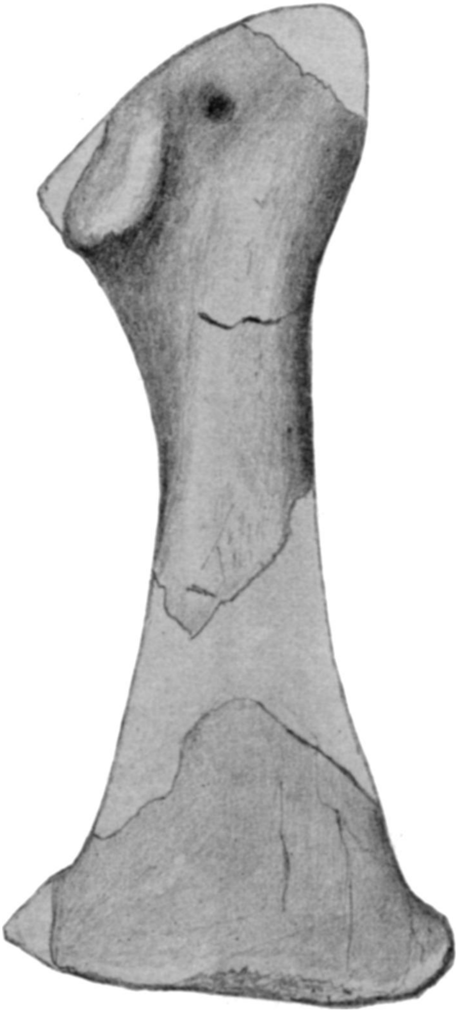

FIG. 4.—*Coelosuchus reedii*. Right coracoid, one-half natural size.

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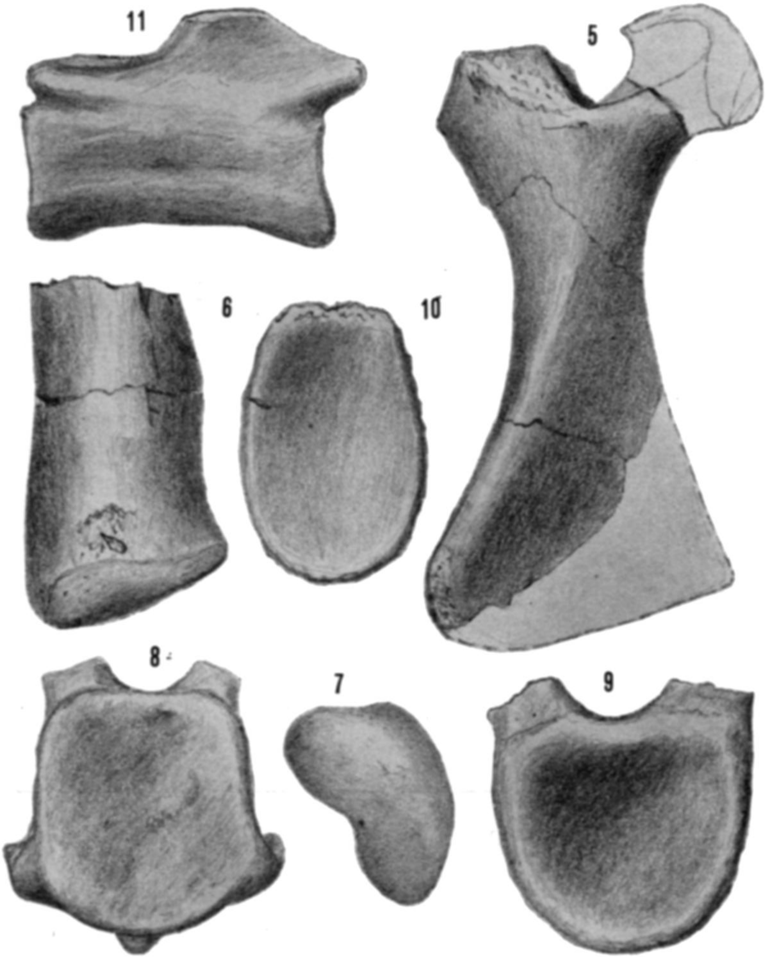
[1] Owen, *Quarterly Journal of the Geological Society*, February, 1879, p. 148.

of late Triassic and Jurassic times, were not as legitimate objects of prey for the amphibious crocodiles as were the small mammals.



Figs. 5–11.—*Coelosuchus reedii.* All two-thirds natural size. Fig. 5, left ischium, Fig. 6, distal extremity of left tibia; Fig. 7, distal face of same; Fig. 8, proximal face of cervical vertebra; Fig. 9, proximal face of dorsal vertebra; Fig. 10, proximal face of dorsal vertebra; Fig. 11, caudal vertebra.

The terrestrial and amphibious crocodiles, with short, broad heads, are yet to be discovered in the Triassic rocks, probably as low as the Muschelkalk.

Just what has been the cause in each case of the change from amphicœlous to procœlous or opisthocœlous vertebræ may not be apparent, but it is no more difficult to believe that this change occurred in the different phyla of crocodiles than in the different orders of reptiles. We know that all procœlian reptiles cannot be traced back to a common procœlian ancestry. The earliest vertebræ of this type were apparently those of the Rhaetic or Liassic pterodactyls. Many of the squamata had changed from amphicœlian to procœlian by the close of the Jurassic times, and it is not at all improbable that the beginning of the change in the crocodiles occurred about this time; certainly so, if the vertebræ described by Seeley from the Wealden are really those of crocodiles, as seems probable.

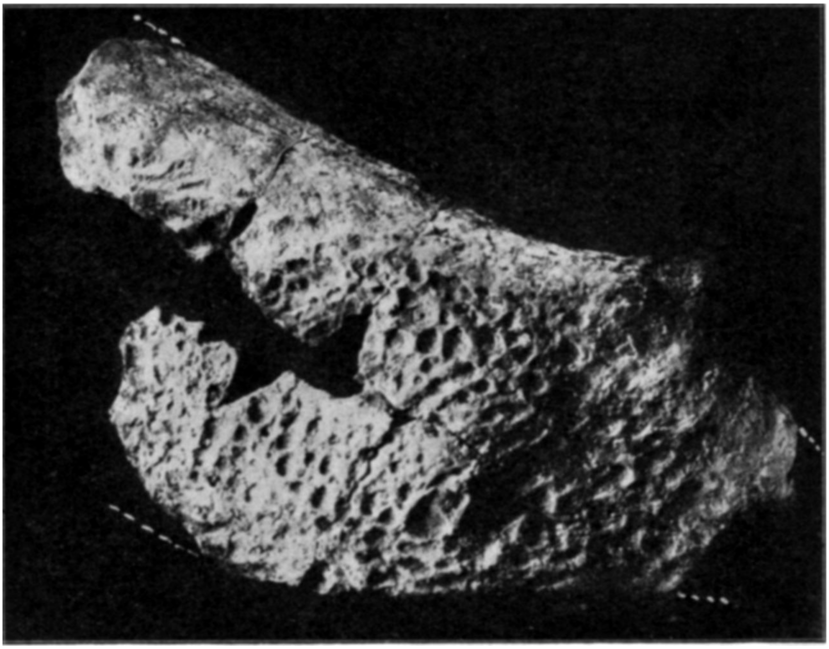


FIG. 12.—*Coelosuchus reedii.* Posterior portion of left mandible, one-eighth natural size.

The geckos among the lizards, chiefly climbing or pendent animals in habit, have retained amphicœlous vertebræ, long after their loss by terrestrial lizards—a fact which does not render their separation from other lacertilia into a distinct suborder imperative. Toads, the most terrestrial of all amphibia probably, have procœlous vertebræ.

The procœlous structure has never been attained by either aquatic or highly amphibious forms; on the contrary, the amphicœlous structure has persisted longest in such. Its attainment has always been correlated with the use of the hind limbs in the support or propulsion of the body upon land, and the amphicœlous structure has lingered longest in the tails, as in the dinosaurs and pterodactyls. The ichthyosaurs, with feeble hind limbs, retained a very primitive structure of the vertebræ, till late in Cretaceous times, until nearly all other reptiles had acquired convexo-concave vertebræ; while the plesiosaurs, equally aquatic animals, and doubtless derived from nearly as primitive ancestors, acquired in many cases truly amphiplatyan vertebræ—a fact doubtless to be correlated with the important use of the hind legs and a well-developed sacrum. The procœlous vertebræ of the mosasaurs was a character acquired by their ancestral terrestrial forbears, as was also their scaled skin. A consideration of these facts, together with the pterygoidal inclusion of the posterior nares, serving no apparently useful purpose in such purely ichthyophagous reptiles, inclines me to the belief that the modern gavials are late descendants of the more terrestrial procœlian types such as *Thoracosaurus* or *Holops* may have been. The opisthocœlous type of vertebra is of much wider distribution, and has been acquired by purely aquatic animals such as *Lepidosteus* and the true salamanders.

No form of convexo-concave vertebræ is of profound morphological significance in the evolution of the vertebrates, but I would not go quite so far as does Koken in uniting procœlian and amphicœlian crocodiles in the same family, notwithstanding the extraordinary resemblance of other parts of the skeleton.[1]

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[1] Koken, *Zeitschrift der Deutschen geologischen Gesellschaft*, 1888, p. 768.